

Learned magnetic map cues and two mechanisms of magnetoreception in turtles

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Growing evidence indicates that migratory animals exploit the magnetic field of the Earth for navigation, both as a compass to determine direction and as a map to determine geographical position¹. It has long been proposed that, to navigate using a magnetic map, animals must learn the magnetic coordinates of the destination^{2,3}, yet the pivotal hypothesis that animals can learn magnetic signatures of geographical areas has, to our knowledge, yet to be tested. Here we report that an iconic navigating species, the loggerhead turtle (*Caretta caretta*), can learn such information. When fed repeatedly in magnetic fields replicating those that exist in particular oceanic locations, juvenile turtles learned to distinguish magnetic fields in which they encountered food from magnetic fields that exist elsewhere, an ability that might underlie foraging site fidelity. Conditioned responses in this new magnetic map assay were unaffected by radiofrequency oscillating magnetic fields, a treatment expected to disrupt radical-pair-based chemical magnetoreception^{4–6}, suggesting that the magnetic map sense of the turtle does not rely on this mechanism. By contrast, orientation behaviour that required use of the magnetic compass was disrupted by radiofrequency oscillating magnetic fields. The findings provide evidence that two different mechanisms of magnetoreception underlie the magnetic map and magnetic compass in sea turtles.

Diverse animals migrate immense distances between specific areas used in foraging, reproduction and seasonal sheltering^{7–9}. How long-distance migrant animals navigate to specific locations has remained enigmatic, but the ability to exploit the magnetic field of the Earth as a source of both directional information (that is, for a magnetic compass sense) and positional information (that is, for a magnetic map sense) is an important element in the navigational repertoire of many species^{1,8,10}.

Magnetically sensitive animals can derive compass information either from the direction (polarity) of field lines or from the relationship between the tilt of magnetic field lines and gravity¹⁰. Magnetic map information can be derived from several geomagnetic parameters that vary predictably across the globe, including the intensity, or strength, of the field and the inclination angle (the angle formed between magnetic field lines and the surface of the Earth)¹. The particular magnetic field parameters that exist at a location, which are sometimes collectively referred to as the ‘magnetic signature’ or ‘magnetic coordinates’ of a site, can potentially provide an animal with a way to recognize a place and return to it^{11–13}.

Navigating to a known destination with a magnetic map presumably requires an animal to learn and remember the magnetic signature of the goal^{2,3,12,13}. Nevertheless, despite strong evidence that sea turtles and other animals possess magnetic maps¹, an ability to learn the magnetic signature of a location has yet to be demonstrated. Here we describe a new behavioural assay in an iconic navigating species, the loggerhead turtle (*C. caretta*), that relies on the ability of turtles to detect magnetic

map information. Our work provides direct evidence that an animal can learn and remember the natural magnetic signature of a geographical area. This ability may enable turtles and other animals to learn the locations of ecologically important destinations and return to them after long migrations.

A noteworthy feature of this new magnetic map assay is that turtles respond to learned magnetic signatures without using the magnetic compass; thus, the new assay effectively decouples the magnetic map and compass senses. We used this decoupling to explore two major questions of magnetic navigation research: first, how sea turtles and other animals sense the magnetic field of the Earth, and second, whether the same biophysical mechanism underlies the magnetic map and compass. Using the magnetic map assay in combination with a second, established assay that requires the magnetic compass, we report strong evidence that two different mechanisms of magnetoreception exist in sea turtles.

Learning magnetic signatures (map assay)

Sea turtles are renowned for their long-distance migrations and extraordinary navigational abilities. At the beginning of their lives, loggerhead turtles respond to magnetic signatures along their transoceanic migratory route by swimming in directions that help them to remain within favourable ocean currents and advance along the migratory pathway^{14,15}. Following this initial migration, turtles take up residence

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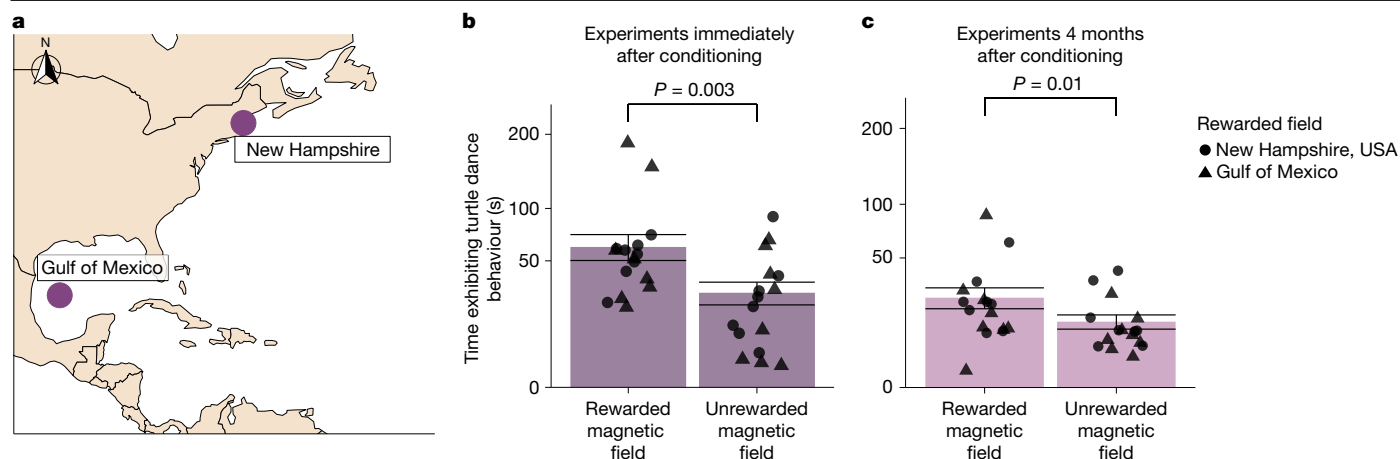


Fig. 1 | Results from conditioning experiments in which turtles learned to discriminate between magnetic fields replicating those that exist near New Hampshire, USA, and in the Gulf of Mexico. **a**, Map showing relative locations of the two treatment fields. The map was created using Natural Earth (<https://www.naturalearthdata.com>; credit Tom Patterson and Nathaniel Vaughn Kelso). **b**, In tests conducted immediately after the conditioning period, turtles exhibited significantly higher levels of turtle dance behaviour when experiencing the field in which they had been fed (two-tailed Wilcoxon signed-rank test, $w = 123$, $P = 0.003$, Hedge's $g = 0.88$, $n = 16$). See Methods for

details of analysis. **c**, Turtles were tested a second time, 4 months after the initial experiments, without experiencing either the rewarded or unrewarded field in the interim. Turtles still discriminated between the two fields (two-tailed Wilcoxon signed-rank test, $w = 118$, $P = 0.01$, Hedge's $g = 0.62$, $n = 16$). Error bars represent s.e.m. To facilitate plotting the large range of responses from individuals, the vertical axis is presented with a square-root transformation to improve visibility of individual data points. Extended Data Fig. 1 shows the same data plotted on a linear scale.

in widely dispersed feeding areas¹⁶. Individual turtles often display strong fidelity to their feeding sites, returning to them repeatedly after seasonal migrations and forced displacements^{17,18}.

To determine whether turtles can learn the magnetic signature of a geographical area where they encounter food, we conditioned captive juvenile loggerheads by feeding them in a magnetic field that replicates one from a specific oceanic location. During the 2 months of conditioning, turtles were fed in one magnetic field (the rewarded field) but were also subjected to an equivalent number of conditioning sessions with a second magnetic signature in which the turtles were not fed (the unrewarded field). Thus, turtles spent equal amounts of time in two magnetic fields, but received food in only one of them. At the end of conditioning, behavioural tests were conducted to assess whether turtles had learned to discriminate between the rewarded and unrewarded magnetic fields (see Methods). Observers blind to the magnetic field treatment analysed video recordings and quantified the amount of time during which each turtle exhibited 'turtle dance' behaviour, a distinctive pattern of movement displayed by captive sea turtles anticipating food. Hallmarks of the behaviour include some or all of the following: tilting the body vertically, holding the head near or above water, opening the mouth, rapid alternating movement of the front flippers, and, occasionally, even spinning in place, hence the name 'turtle dance' (Supplementary Video 1).

In an initial experiment, turtles were conditioned to distinguish between two magnetic signatures that represented similar magnetic changes (in terms of inclination and intensity) to the south and north of the testing site in North Carolina, USA. The south field approximated that of a location in the Gulf of Mexico and the north field approximated a location near New Hampshire, USA (Fig. 1a and Extended Data Table 2). Half of the turtles received food only in the Gulf of Mexico field and half only in the New Hampshire field. After conditioning, turtles were exposed to the two magnetic fields in the absence of food. Turtles exhibited significantly higher levels of turtle dance behaviour when experiencing the field in which they had been fed (Fig. 1b; Wilcoxon signed-rank test, $w = 123$, $P = 0.003$, Hedge's $g = 0.88$). The turtles continued to distinguish between the two fields when tested 4 months later, without being conditioned to either field in the interim (Fig. 1c; Wilcoxon signed-rank test, $w = 118$, $P = 0.01$, Hedge's $g = 0.62$).

These results suggest that turtles can learn to associate food with a specific magnetic signature and retain this learned association for several months.

To investigate the robustness of this response, several replicates of this experiment were conducted using different groups of turtles and different pairs of magnetic fields. A second group of turtles was conditioned to distinguish between magnetic fields that exist near the coasts of Cuba and Delaware, USA. These turtles exhibited significantly higher levels of turtle dance behaviour when exposed to their rewarded magnetic field, indicating that they could recognize the magnetic field (Fig. 2a; Wilcoxon signed-rank test, $w = 108$, $P = 0.04$, Hedge's $g = 0.50$). A third cohort was conditioned to discriminate between magnetic fields that exist near the coast of Florida, USA, and Maine, USA. Turtles again learned to differentiate between the two magnetic fields (Fig. 2b; Wilcoxon signed-rank test, $w = 121$, $P = 0.004$, Hedge's $g = 0.63$).

To investigate whether turtles can learn to associate food with more than one magnetic field, the third cohort (the same group previously conditioned to Florida versus Maine) was conditioned a second time, using two magnetic fields that exist north of the test site, one near Virginia, USA, and the other near Newfoundland, Canada. Turtles learned to discriminate between these two fields as well (Fig. 2c; Wilcoxon signed-rank test, $w = 115$, $P = 0.01$, Hedge's $g = 0.60$).

A fourth cohort of turtles was conditioned to distinguish between magnetic fields that exist at two Caribbean locations that are both south of the test site and relatively close to each other (approximately 300 km apart), one near Haiti and the other near the Turks and Caicos Islands. Yet again, turtles learned to recognize the magnetic field in which they encountered food (Fig. 2d; Wilcoxon signed-rank test, $w = 97$, $P = 0.003$, Hedge's $g = 0.60$).

An analysis of the cumulative data from all experiments demonstrated that turtles are capable of associating food with magnetic signatures (Fig. 3a; Wilcoxon signed-rank test, $w = 2,676$, $P = 1.6 \times 10^{-8}$, Hedge's $g = 0.50$). As a complementary way of analysing the data, the percentage change in turtle dance behaviour in the rewarded field was calculated relative to the unrewarded field for each individual turtle. If a turtle increased its dance behaviour compared with its own baseline response in the unrewarded field, then the percentage

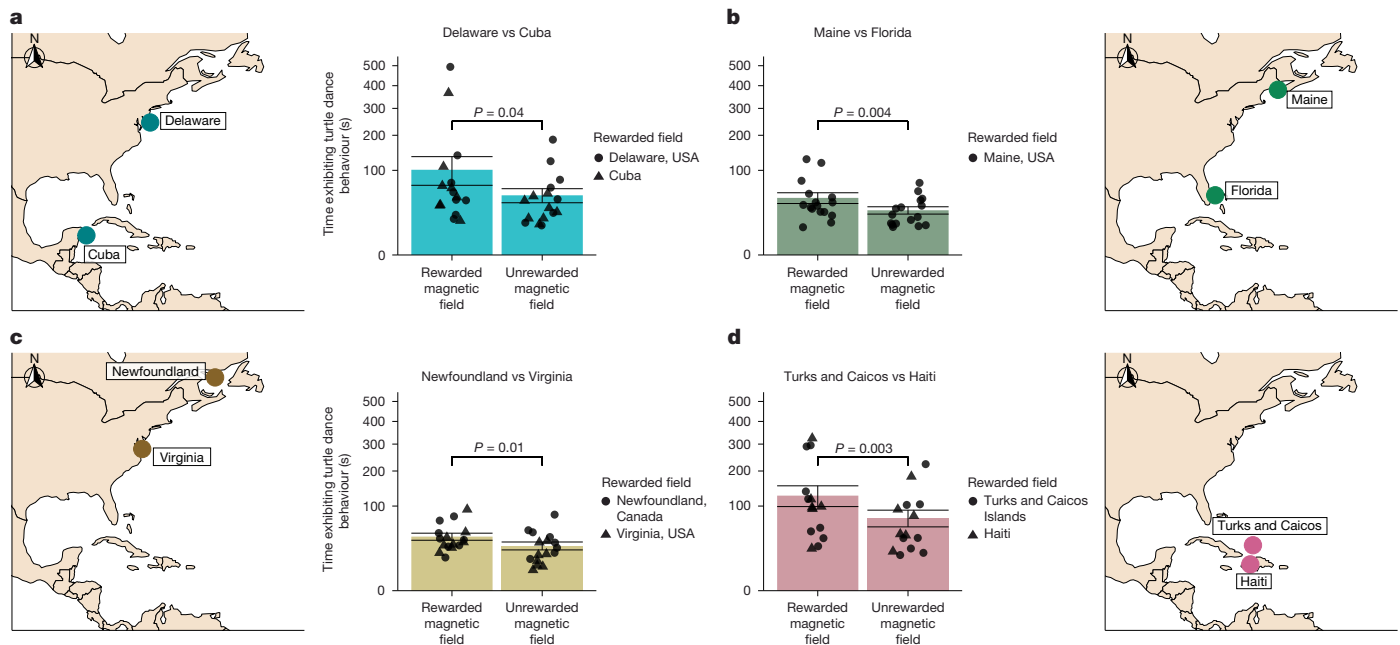


Fig. 2 | Results of four additional map assay experiments, in which turtles discriminated between a magnetic field in which they were fed and a magnetic field in which they were not. a–d. Turtles differentiated between magnetic fields that exist near: Delaware, USA, and Cuba (a; two-tailed Wilcoxon signed-rank test, $w = 108$, $P = 0.04$, Hedge's $g = 0.50$, $n = 16$); Maine and Florida, USA (b; two-tailed Wilcoxon signed-rank test, $w = 121$, $P = 0.004$, Hedge's $g = 0.63$, $n = 16$); Newfoundland, Canada and Virginia, USA (c; two-tailed Wilcoxon signed-rank test, $w = 115$, $P = 0.01$, Hedge's $g = 0.60$, $n = 16$); and the Turks and

Caicos Islands and Haiti (d; two-tailed Wilcoxon signed-rank test, $w = 97$, $P = 0.003$, Hedge's $g = 0.60$, $n = 14$). The data in c represent a second conditioning experiment conducted with the same turtles used in b and thus indicate that turtles can learn magnetic fields that exist at multiple locations. Remaining conventions are as in Fig. 1. Extended Data Fig. 2 shows the same data plotted on a linear scale. The maps were created using Natural Earth (<https://www.naturalearthdata.com>; credit Tom Patterson and Nathaniel Vaughn Kelso).

change in the dance response should exceed zero. An analysis of all data indicated that the percentage change in turtle dance behaviour was significantly greater than 0 (Fig. 3b; one-tailed Wilcoxon signed-rank test, $w = 2,833$, $P = 6.2 \times 10^{-11}$, Hedge's $g = 0.55$). Results have also been plotted for each pair of magnetic fields tested and similarly demonstrate that, for all pairs of fields, turtle dancing in the rewarded field showed a percentage change greater than zero relative to the unrewarded field (Extended Data Fig. 4). Thus, turtles showed more turtle dance behaviour in the rewarded field than in the unrewarded field, indicating that turtles can learn to recognize particular magnetic fields.

Several studies have established that recognition of magnetic signatures by sea turtles and other animals requires simultaneous perception of both magnetic inclination and intensity^{15,19,20}. Nevertheless, turtles in the present experiments might hypothetically have distinguished between fields by using a single magnetic parameter (that is, inclination or intensity) rather than both together. To investigate this possibility, turtles were presented with fields in which the geomagnetic parameters of the rewarded and unrewarded fields were mismatched; that is, the inclination angle of the rewarded field was paired with the intensity of the unrewarded field and vice versa (Fig. 4a). We reasoned that, if one matching parameter instead of two is sufficient for recognition, then turtles should respond to the mismatched fields as they do to the rewarded field. Turtles that had been conditioned to discriminate between magnetic fields that exist near Maine and Florida were presented with: (1) one of the two mismatched fields, (2) the rewarded field (Maine), and (3) the unrewarded field (Florida). Results from a linear mixed effects model (Methods) indicated that, as in previous experiments, turtles displayed significantly more turtle dancing in the rewarded field than in the unrewarded field (Benjamini–Hochberg pairwise comparisons, $P = 0.01$, Hedge's $g = 0.97$; Fig. 4b). Similarly, turtles responded significantly more to the rewarded field than to the 'mismatched' magnetic fields (Benjamini–Hochberg

pairwise comparisons, $P = 0.01$, Hedge's $g = 0.67$). No difference existed between the responses to the mismatched and unrewarded fields (Fig. 4b). These results are consistent with the interpretation that both inclination and intensity must match the rewarded field for turtles to respond.

The percentage change in turtle dancing was also calculated for each individual turtle in the rewarded and mismatched fields, relative to its response in the unrewarded field (Fig. 4c). As expected, turtles in the rewarded field showed percentage increases significantly greater than 0, indicating that the rewarded magnetic signature elicited increased turtle dancing (one-tailed Wilcoxon signed-rank test, $w = 133$, $P = 0.00008$, $n = 16$). By contrast, for each mismatched field, the percentage change in turtle dancing was not significantly greater than zero, suggesting that neither mismatched field (and thus neither inclination alone nor intensity alone) was recognized as the rewarded field. Equivalence testing confirmed that responses of turtles to the rewarded and mismatched fields were not equivalent (Methods and Fig. 4c), consistent with the interpretation that turtles use both inclination and intensity together.

Overall, the results provide strong evidence that loggerhead turtles can learn the magnetic signatures of specific geographical areas. Such an ability has, to our knowledge, never before been demonstrated in any animal. In total, turtles were presented with five different pairs of magnetic fields that varied in both geographical and magnetic distance between the constituent fields. In each case, turtles learned to distinguish between the rewarded and unrewarded field, regardless of whether the replicated sites were both north of the test site, both south of the test site, or whether one site was north and the other was south.

Role of learning in site fidelity

Sea turtles are widely presumed to learn the location of foraging areas to which they subsequently migrate^{21–23}. Our findings are consistent

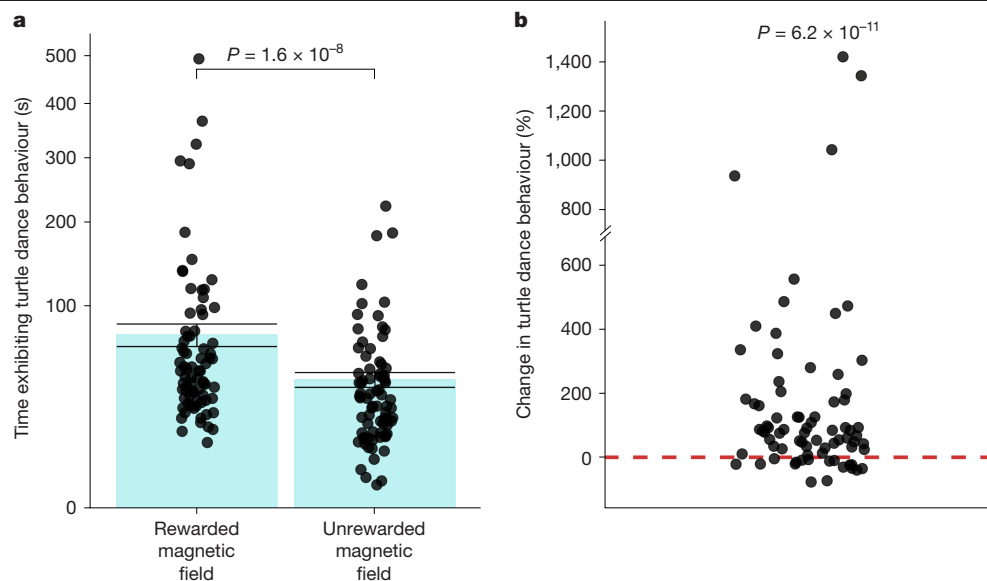


Fig. 3 | Data from all map assay experiments analysed cumulatively.

a, Turtles learned to discriminate between a magnetic field in which they received food and one in which they did not (two-tailed Wilcoxon signed-rank test, $w = 2,676$, $P = 1.6 \times 10^{-8}$, Hedge's $g = 0.50$, $n = 78$). Each dot represents an individual response. Remaining conventions are as in Fig. 1. Extended Data Fig. 3 shows the same data plotted on a linear scale. **b**, Percentage change in turtle dancing responses in the rewarded field relative to the unrewarded field

for all conditioned turtles. For each turtle, percentage change was defined as: $\frac{\text{Rewarded field turtle dancing} - \text{unrewarded field turtle dancing}}{\text{unrewarded field turtle dancing}} \times 100$. The red dashed line indicates a 0% change in turtle dancing behaviour relative to the unrewarded field. The dots represent the percentage change in turtle dancing for individual turtles. The percentage change in turtle dancing behaviour was significantly greater than 0 (one-tailed Wilcoxon signed-rank test, $w = 2,833$, $P = 6.2 \times 10^{-11}$, Hedge's $g = 0.55$, $n = 78$).

with the hypothesis that turtles use learned magnetic fields to help them navigate to and recognize feeding destinations. Under natural conditions, successful foraging may prompt a turtle to notice and remember the magnetic signature of a feeding area, enabling turtles to subsequently return to such areas using a magnetic map²². The flexibility of such a system may confer considerable survival value in a marine environment where the optimal feeding habitat is restricted to specific, widely dispersed geographical locations.

If turtles use magnetic signatures when returning to foraging sites after migrations, then they presumably must be able to retain this information for at least several months. For example, adult female loggerheads return to their foraging grounds after months-long reproductive migrations¹⁸. Similarly, juvenile loggerhead turtles migrate seasonally to and from coastal feeding areas located in temperate waters²⁴. Our results demonstrate that turtles can remember the magnetic signature of an area over time spans relevant to their migration patterns; turtles continued to recognize the magnetic field in which they had been fed 4 months after the conditioning period, despite having no additional exposure to the learned magnetic field (Fig. 1c).

Results also demonstrate that turtles can learn the magnetic signatures associated with more than one location (Fig. 2b,c). An ability to learn magnetic signatures of multiple feeding sites is likely to be adaptive, given that some turtles use multiple foraging areas in different geographical locations during different seasons^{24,25}. In addition, many turtles change foraging areas as they mature²⁶ and some are forced to relocate when formerly favourable feeding grounds become uninhabitable²⁶.

The ability of turtles to learn magnetic signatures suggests that turtles might be able to build and rebuild their magnetic maps as they gain experience. For example, although whether turtles use learned magnetic signatures in navigation was not directly addressed by this work, the results indicate that turtles can learn new magnetic fields as would be required to incorporate new locations, such as a new foraging area, into a magnetic map. In addition, turtles might use this ability to help compensate for secular variation, that is, the gradual change

of the magnetic field of the Earth, by relearning the magnetic field of the target site at each visit²⁷. Recognition of foraging areas and other targets might also be aided by the use of multiple, non-magnetic cues, especially close to the goal^{27–29}.

Mechanism of magnetic field detection

Despite recent progress¹⁰, the biophysical mechanism or mechanisms underlying the magnetic map and compass senses have not been determined unequivocally in any animal. Several different mechanisms of magnetoreception have been discussed^{30,31}. Among these is the chemical magnetoreception or radical pair hypothesis, which proposes that light-induced chemical reactions enable animals to detect the magnetic field of the Earth^{4,32,33}. The putative process is initiated by light exciting an electron transfer between two molecules, resulting in unstable radical pairs whose electron spin states are influenced by the magnetic field of the Earth; the resulting spin states then affect reaction products that might provide animals with magnetic field information. Such reactions have been proposed for cryptochrome, a photoreceptive protein^{34–36}, but other pathways are also possible^{37,38}.

Oscillating magnetic fields in the radiofrequency range are predicted to disrupt transitions between electron spin states and thus might impair the ability of an animal to sense magnetic fields⁴. A common test for chemical magnetoreception therefore involves determining whether radiofrequency fields disrupt behaviour that depends on magnetoreception^{4–6}. We investigated the effect of radiofrequency fields on both the magnetic map sense and the magnetic compass sense of turtles, first using the new map assay and then using a second behavioural assay that requires the magnetic compass.

Radiofrequency fields and the map sense

The map assay experiment was conducted with turtles conditioned to discriminate between a rewarded magnetic field that exists in Maine and

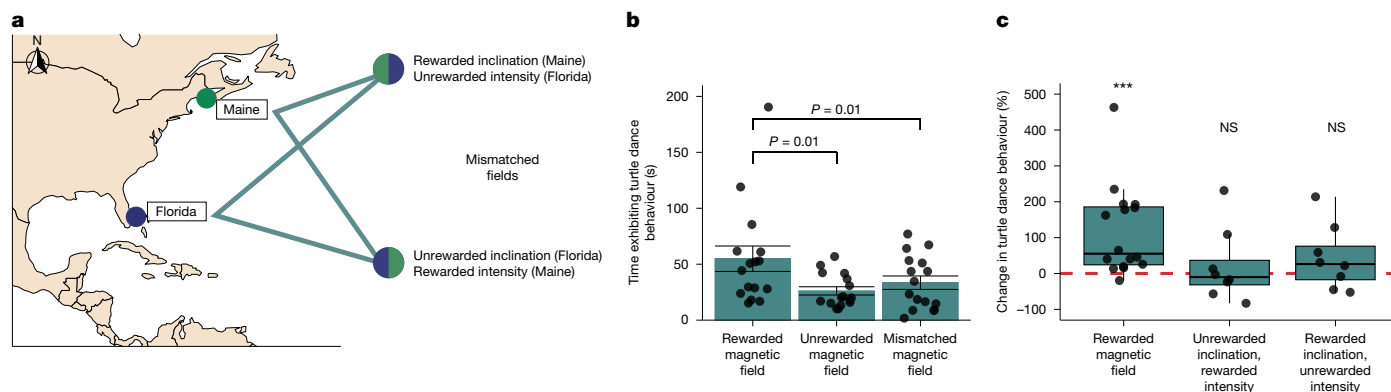


Fig. 4 | Mismatched field experiments. **a**, Experimental design. Turtles conditioned to discriminate between magnetic fields near Maine and Florida (see Fig. 2b) were exposed to three magnetic fields: the rewarded field, the unrewarded field and one of two mismatched fields, consisting either of rewarded inclination and unrewarded intensity or unrewarded inclination and rewarded intensity. The map was created using Natural Earth (<https://www.naturalearthdata.com>; credit Tom Patterson and Nathaniel Vaughn Kelso). **b**, Amount of time spent turtle dancing. The field treatment was a significant predictor of time spent turtle dancing (see Extended Data Table 1; analysis of variance, $F(2,30) = 5.9$, $P = 0.007$). Benjamini–Hochberg pairwise comparisons indicated that turtles danced significantly longer in their rewarded field than in the unrewarded field ($P = 0.01$, Hedge’s $g = 0.97$) or to the mismatched fields ($P = 0.01$, Hedge’s $g = 0.67$); responses to the mismatched fields and the unrewarded field did not differ ($P = 0.9$, Hedge’s $g = 0.032$). Conventions are

as in Fig. 3. **c**, Percentage change in turtle dancing behaviour relative to the unrewarded field. The red dashed line indicates a 0% change. One-tailed Wilcoxon signed-rank tests indicate that the percentage change significantly exceeded 0 for the rewarded field ($w = 133$, $***P = 0.00008$, Hedge’s $g = 0.88$, $n = 16$), but not for either of the mismatched fields ($w = 17$, $P = 0.58$, Hedge’s $g = 0.18$, $n = 8$ for the unrewarded inclination and rewarded intensity field; $w = 26$, $P = 0.16$, Hedge’s $g = 0.42$, $n = 8$ for the rewarded inclination and unrewarded intensity field). Responses to the rewarded field were not equivalent to the responses to either of the mismatched fields (unrewarded inclination and rewarded intensity: Wilcoxon two one-sided tests (TOST), $w = 50$, $P = 0.20$); rewarded inclination and unrewarded intensity field: Wilcoxon TOST, $w = 44$, $P = 0.12$). The black dots represent individual responses. The boxes span the first to third quartile, the centre line represents the median, and the whiskers represent the 5th and 95th percentiles. NS, not significant.

an unrewarded field from Florida (Fig. 2b). These turtles were tested again in the rewarded Maine field, with and without broadband radiofrequency fields in the 0.1–10 MHz range known to disrupt magnetic sensing in birds and other animals⁶. No difference was observed in turtle responses when radiofrequency fields were present or absent (Wilcoxon signed-rank test, $w = 65$, $P = 0.9$, Hedge’s $g = 0.074$; Fig. 5a). These results are consistent with the interpretation that the magnetic map sense of sea turtles is unaffected by radiofrequency fields and thus does not rely on chemical magnetoreception.

Compass sense and radical pair mechanism

A second experiment investigated the effect of radiofrequency fields on navigation behaviour that requires the simultaneous use of both the magnetic map and the magnetic compass senses. This second assay, referred to as the ‘compass and map assay’, relied on spontaneous orientation responses of newly hatched loggerhead turtles to magnetic fields along their migratory route¹⁴. Young loggerhead turtles from Florida gradually travel around the north Atlantic Ocean before returning to North American waters¹⁴. Hatchlings achieve this migration in part by using their magnetic map sense to identify magnetic signatures encountered along the route and then using their magnetic compass sense to swim in appropriate directions to help them progress along the migratory pathway^{14,15}.

In this experiment, we relied on the responses of turtles to a magnetic field that exists near the Cape Verde Islands, an archipelago located off the west coast of Africa. Turtles in a previous experiment responded to this field with southwesterly orientation, a direction that presumably facilitates movement back towards North America and helps them to avoid the south-flowing Guinea Current, which may sweep them out of their normal range¹⁹. As in the map assay experiments, turtles were tested both in the presence and in the absence of a broadband radiofrequency field that encompassed frequencies ranging from 0.1 to 10 MHz. The orientation responses of hatchlings were monitored using standard techniques^{14,15,19}. In brief, each turtle was tethered to an electronic tracking unit in the centre of a water-filled,

circular arena surrounded by a magnetic coil system, which could be used to replicate the magnetic field that exists anywhere in the Atlantic Ocean^{14,15,19}. After tethering, each turtle swam towards a light (wavelength range of approximately 420–750 nm) for 10 min in the local magnetic field. The light was then turned off and the magnetic field was changed to the Cape Verde field. After a 3-min acclimation period, the radiofrequency generator was either activated or left off, and the orientation of the turtle was recorded for 5 min as it swam in total darkness.

Turtles exposed to the Cape Verde magnetic field in the absence of radiofrequency fields swam approximately westwards and were significantly oriented (Rayleigh test, $r = 0.53$, $P = 0.0004$, mean angle = 293.1° , $n = 26$; Fig. 5b). By contrast, turtles exposed to the Cape Verde field in the presence of radiofrequency fields had orientation that was statistically indistinguishable from random (Rayleigh test, $r = 0.19$, $P = 0.42$, mean angle = 47.9° , $n = 24$; Fig. 5b). The two distributions were significantly different (Watson test, $U^2 = 0.35$, $P < 0.01$), indicating that radiofrequency fields had an effect on turtle orientation.

The compass and map assay requires that turtles use both a map sense and a compass sense. Given that the responses of turtles were not altered by radiofrequency fields in the map assay experiments, the effect of radiofrequency fields in the compass and map assay experiments is consistent with the interpretation that radiofrequency fields affected the magnetic compass alone. The results from both assays thus suggest that two different mechanisms of magnetoreception probably exist in sea turtles: a mechanism underlying the compass sense that is disrupted by radiofrequency fields, and a mechanism underlying the map sense that is not. A reasonable working hypothesis is that the compass sense relies on chemical magnetoreception, whereas the map sense relies on an alternative mechanism.

Role of light in the magnetic compass

If the magnetic compass of turtles indeed depends on chemical magnetoreception, it is interesting to note that the compass functions in total darkness. The prevailing model of chemical magnetoreception

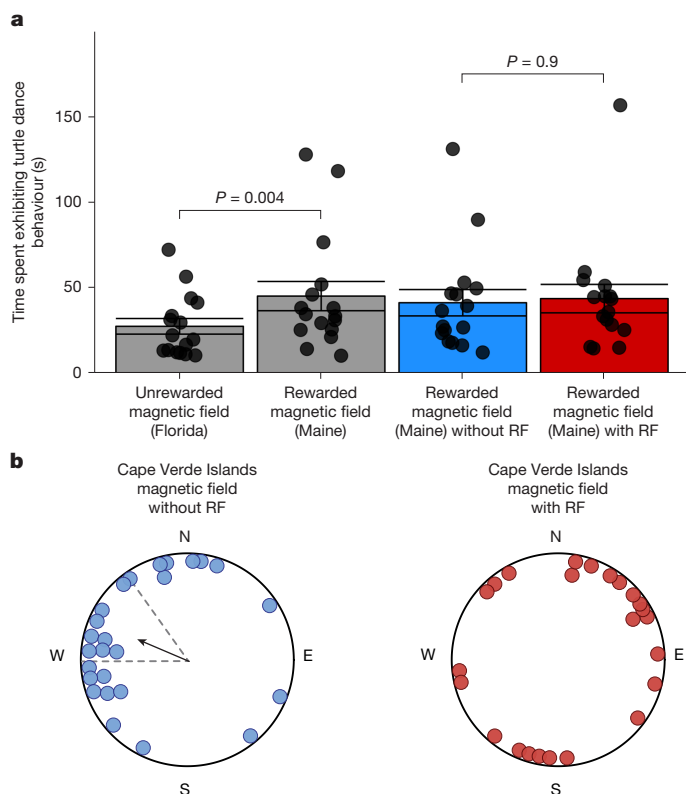


Fig. 5 | Results of experiments with oscillating magnetic fields in the radiofrequency range (radiofrequency field experiments). **a**, Results of the map assay. Responses to the initial behavioural tests showed that turtles successfully learned to discriminate between magnetic fields that exist near Maine (the rewarded field) and near Florida (the unrewarded field); these data (grey bars) are reproduced from Fig. 2b as a convenient reference. In the radiofrequency field experiments, responses to the rewarded field did not differ regardless of whether radiofrequency (RF) was absent (blue bar) or present (red bar; two-tailed Wilcoxon signed-rank test, $w = 65$, $P = 0.9$, Hedge's $g = 0.076$, $n = 16$). Each dot represents results from a single individual. Conventions are as in Fig. 3. **b**, Results from the compass and map assay. Turtles exposed to a magnetic field that exists near the Cape Verde Islands swam approximately westwards and were significantly oriented (Rayleigh test, $r = 0.53$, $P = 0.0004$, mean angle = 293.2° (95% CI = 269.5 – 324.5°), $n = 26$, left circular plot). Turtles exposed to the same Cape Verde field but with radiofrequency present had orientation statistically indistinguishable from random (Rayleigh test, $r = 0.19$, $P = 0.42$, mean angle = 47.9° , $n = 24$, right circular plot). The two distributions were significantly different (Watson test, $U^2 = 0.35$, $P < 0.01$). The dots represent the swimming directions of individual turtles; in the left circular diagram, the black arrow represents the mean swimming direction of the entire group, and the dashed lines represent 95% confidence intervals. Data are plotted relative to magnetic north. In **a**, **b**, blue indicates treatments without radiofrequency fields, and red corresponds to treatments with radiofrequency fields.

proposes that a series of chemical reactions begins when light excites an electron transfer, creating radical pairs; thus, in this scenario, light must be present for an animal to detect magnetic fields. Consistent with this hypothesis, several animals, including birds and monarch butterflies, require specific wavelengths of light to respond to magnetic stimuli and thus show light-dependent magnetoreception^{33,35}. By contrast, other animals such as sea turtles and fishes have light-independent magnetoreception and orient magnetically in darkness^{14,39,40}. Several authors have proposed that light dependence indicates chemical magnetoreception and light independence indicates an alternate mechanism^{32,40,41}. In such a paradigm, animals with light-independent magnetoreception are not expected to be affected by radiofrequency fields.

The finding that the light-independent compass of turtles is nonetheless sensitive to radiofrequency fields is seemingly incompatible

with the standard paradigm. It has been proposed, however, that light activates a sequence of chemical magnetoreception reactions that, once initiated, can continue afterwards for minutes or hours in darkness, with the crucial magnetoreceptive steps not requiring light once the reactions are set in motion^{42,43}. In this context, it is noteworthy that turtles were exposed to a white LED for 10 min before being tested in darkness (Methods), although whether light exposure was necessary for subsequent magnetoreception in darkness remains unknown.

It is also noteworthy that, despite apparent differences in light dependence, the bird and turtle magnetic compasses share properties that might reflect a common underlying mechanism. Not only are both systems disrupted by radiofrequency fields but both are also inclination compasses insensitive to field polarity^{10,44}.

Alternative magnetoreception hypotheses

Given that the magnetic map sense in turtles is unlikely to rely on chemical magnetoreception, three alternative mechanisms worth considering are: (1) magnetite, (2) the biocompass or MagR model, and (3) electromagnetic induction. The simplest version of the magnetite hypothesis proposes that crystals of single-domain magnetite (Fe_3O_4) provide the physical basis of the magnetic sense by rotating into alignment with the magnetic field of the Earth and, in so doing, activate receptors that initiate a neural response^{30,31,45}. Although no unequivocal evidence for magnetite-based magnetoreceptors has been reported, indirect evidence consistent with the hypothesis has been obtained from studies in which animals were exposed to strong, short magnetic pulses^{46–48}. Such magnetic pulses have the potential to disrupt magnetite-based magnetoreception by reversing the magnetic dipole moment of magnetite crystals. In previous work, hatchling turtles subjected to magnetic pulses oriented randomly when exposed to a magnetic field in which they were expected to swim eastwards⁴⁶. In principle, the pulse might have disrupted the map, the compass, or both. In light of our current results, one possibility is that the magnetic pulse affected the magnetic map sense and that a magnetite-based mechanism underlies the map.

In contrast to the magnetite hypothesis, the biocompass or MagR hypothesis proposes that magnetoreception is achieved through a macromolecular nanostructure composed of an iron–sulfur protein (MagR), polymerized into a linear protein complex and wrapped helically by cryptochromes⁴⁹. This putative magnetoreceptor, which might share some properties with both magnetite crystals and cryptochromes, has been proposed to underlie magnetic sensing in diverse animals⁵⁰, although many details remain unresolved^{38,51}. At present, too little is known about the putative MagR biocompass mechanism to assess with confidence whether radiofrequency fields or magnetic pulses might affect it.

Yet another way that an animal might hypothetically sense magnetic fields is through electromagnetic induction, in which the movement of an animal (or its head) through the magnetic field of the Earth induces a charge separation that the animal can detect^{30,31}. This mechanism was originally proposed to underlie magnetic field detection by sharks and rays, which have specialized electroreceptors that might detect the induced currents generated as the fish swim through the geomagnetic field⁵². More recently, the hypothesis has been extended to birds, but with the postulated receptors located in the semicircular canals⁵³. To our knowledge, the possibility of an induction mechanism based in the inner ear has not yet been investigated in turtles. Similarly, whether radiofrequency fields or magnetic pulses (or the electric fields associated with either) might affect such a mechanism is unknown.

Dual mechanisms of magnetoreception

The magnetic map and magnetic compass often function together in navigational tasks; thus, investigating the mechanism of one

independently from the other can be difficult. Nevertheless, findings consistent with two magnetoreception mechanisms have been reported both for long-distance avian migrants and for amphibians that travel only over short distances^{47,54}. For example, in a species of songbird (the silvereye *Zosterops lateralis*), magnetic pulses failed to disrupt the compass orientation of juveniles but did disrupt orientation of adult silvereyes that were using a map⁴⁷. Given that the bird compass is disrupted by radiofrequency fields^{4,6,55}, the silvereye findings have been interpreted as evidence that birds have a magnetic compass based on chemical magnetoreception and a magnetic map sense based on magnetite^{10,47}. A similar system has been hypothesized in newts⁵⁴.

Our results provide evidence that sea turtles have two mechanisms of magnetoreception. The findings also raise the possibility that turtles and birds, the two groups most thoroughly studied in the context of long-distance navigation, both have magnetic compasses based on chemical magnetoreception. It remains unclear whether the mechanism underlying the magnetic map sense is the same in both instances or, indeed, whether the two groups exploit the same magnetic field parameters in their maps¹. Nonetheless, considered in their totality, the results from three groups of vertebrates (birds, amphibians and now reptiles) suggest that dual magnetoreception systems are common among vertebrates. In principle, dual mechanisms might arise if the optimal way to detect direction differs from the best way to detect magnetic parameters associated with positional information, resulting in two magnetic senses, each optimized for different tasks.

Conclusions

Our results demonstrate that an animal can learn the natural magnetic signatures of geographical areas, thus corroborating a foundational premise of goal navigation with magnetic maps. The ability to learn and remember magnetic signatures may largely explain how sea turtles are able to return reliably to specific foraging areas and nesting beaches after long migrations. A similar ability may be crucial for numerous other animal migrants, including fishes and birds, that also travel long distances to ecologically important locations.

In addition, our results provide evidence that two different biophysical mechanisms underlie the magnetic map and magnetic compass in sea turtles. These findings, combined with results in birds and amphibians, suggest that dual magnetoreception systems may be the rule for migratory vertebrates. Moreover, magnetoreception systems of phylogenetically diverse animals, despite functional differences (for example, light dependence or light independence), and despite being used in different ways over a wide range of spatial scales¹, might be organized in a similar way and share common underlying mechanisms.

Online content

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Methods

This study included two different behavioural assays. Each is described below.

Map assay

Animal collection, care and housing. Loggerhead turtles (*C. caretta*) were collected as hatchlings as they emerged from nests on Bald Head Island, North Carolina, USA. A total of 14–16 hatchlings was collected from 8–10 different nests in August of each year (2017–2020). They were transported to Chapel Hill, NC, USA, where they were maintained until their release the following summer. Turtles were housed in individual tanks in a recirculating artificial seawater system with water temperature maintained between 26 °C and 28 °C. Turtles were fed a gelatin diet (Mazuri) and squid. Because the sex of immature turtles cannot be established without invasive procedures, we did not determine sex for turtles in any of the experiments described in this study.

Map assay experiments were conducted five times between 2017 and 2020 with four different cohorts of turtles (Extended Data Table 2). Three of these groups contained 16 turtles and one contained 14 turtles. Sample sizes were based on both the maximum number of turtles that we could house at one time and the sample sizes used in other reptile conditioning studies⁵⁶. At the time of first conditioning, turtles were approximately 1–2 months of age, with straight carapace length of 4.1–6.4 cm and a mass of 21–48 g. Turtles from the 2019 cohort were conditioned both in the autumn of 2019 and a second time in the spring of 2020, at which time they were approximately 9 months of age with a mass of 675–900 g.

Experimental apparatus. A magnetic coil system was used to produce earth-strength magnetic fields replicating those that exist at various locations within the Atlantic Ocean (Extended Data Table 2). The coil system consisted of three 4-coil systems arranged orthogonally⁵⁷ that allowed control of the magnetic field in three dimensions. The two outer wraps of each coil measured 2.1 m on a side and the two inner wraps measured 2.2 m on a side. Each coil was powered by an independent power supply operated on a constant-current setting. Current to the coil system was set to generate magnetic signatures that matched those of target sites in the Atlantic Ocean (Extended Data Table 2). Field parameters inside the coil were measured with a tri-axial magnetometer (Applied Physics Systems model 520 or Meda model FVM-400; Extended Data Table 2). The magnetic signatures consisted of combinations of inclination and intensity, the two magnetic parameters that turtles and other aquatic animals are known to detect^{15,20,58,59}. Declination (the difference between magnetic north and geographical north) was held constant in all magnetic fields. Whether turtles detect declination is unknown, but measuring declination requires determining geographical north, which in turn requires using celestial cues over time to determine the axis of Earth's rotation¹; thus, because turtles could not see the sky, they could not use declination.

During conditioning, turtles were placed into individual, 20-l cylindrical buckets partially filled with artificial sea water. For most experiments, the buckets were 30 cm in diameter with a water depth of 15 cm. For experiments in spring of 2020, which involved older, larger turtles (see 'Animal collection, care and housing' section), animals were placed into 60-l cylindrical buckets (diameter of 55 cm) filled with artificial sea water to a depth of 30 cm. In all cases, buckets were arranged in the centre of a plywood platform inside the magnetic coil system, with the height of the platform adjusted so that turtles were located where the field generated by the coil system was most uniform⁵⁷. Lighting in the coil was provided by white fluorescent lights (model number 10460, GE) and white LED lights (model number UCL/27/12/26/8/120, GE; colour temperature of 3,000 K, 415 lumens and 91 CRI (colour rendering index) that remained on during conditioning and behavioural experiments because turtles in this age group become inactive in darkness.

Magnetic field conditioning protocol. During the 2-month conditioning period, turtles were exposed repeatedly to two different magnetic fields, each replicating a natural magnetic signature that exists at a specific geographical area in the ocean. In all but one experiment (see below), turtles in each cohort were randomly assigned to one of two groups; each group was subsequently fed only in one of the two magnetic fields. Thus, the magnetic field that served as the rewarded field for one group was the unrewarded field for the other group, and vice versa.

During each day of conditioning, all turtles were exposed to only one of the two magnetic fields. Turtles alternated daily between experiencing the field in which they received food and the field in which they did not. For example, in the first experiment involving magnetic fields that exist near New Hampshire, USA, and in the Gulf of Mexico, one group of turtles was fed on days when the New Hampshire field was used, whereas the other group was not fed. On the following day, when the Gulf of Mexico field was used, the first group of turtles was not fed, but the second group was fed. Thus, turtles in both groups were exposed to both magnetic fields for equivalent periods of time but were fed in only one of the two fields.

This basic pattern was repeated for all years except 2019 when, to increase the sample size for the mismatched field and radiofrequency experiments (see below), all turtles were fed in a magnetic field that exists near the coast of Maine, USA, and were not fed when exposed to a magnetic field that exists near the coast of Florida, USA. The pairs of magnetic fields used in each conditioning experiment are summarized in Extended Data Table 2.

Conditioning was conducted daily over a period of 2 months. During conditioning sessions, each turtle was placed into its own individual bucket and the buckets were arranged inside the magnetic coil system near the centre, where the field from the coil was most uniform. Once inside the coil, turtles were allowed to acclimate for 20 min in a magnetic field similar to one that exists in the facility where the turtles were housed (the acclimation field; Extended Data Table 2). After the acclimation period, the group was exposed to one of the two magnetic signatures for 40 min.

During conditioning sessions in which turtles received food, the food was added to a bucket for each turtle 5–15 min after the field was changed. Thus, turtles had the remainder of the 40-min period to locate and consume the food while in their rewarded field. During sessions in which turtles were not fed, turtles remained in the unrewarded field for 40 min but did not receive food, either during the session or later that day. During the 2-month conditioning period, turtles did not receive any food except during sessions in which they experienced their rewarded field. In addition, because turtles can detect airborne odorants from food⁶⁰, the odours of food were not introduced into the room except when turtles were fed in their rewarded field.

Magnetic field discrimination protocol. After 2 months of daily conditioning sessions, turtles were tested in both magnetic fields to determine whether they could discriminate between them in the absence of food. To eliminate the possibility that the behaviour of one turtle might influence that of another, each turtle was placed into its bucket and tested alone inside the magnetic coil system, with no other turtles present in the coil or room. Conditions were otherwise identical to those used in conditioning, except that no food was provided at any time.

Trials were conducted over 4 consecutive days. Each turtle experienced two trials: one in the rewarded field and one in the unrewarded field. Half of the turtles were tested in their rewarded field first and half in the unrewarded field first. Because each turtle had been fed every other day during conditioning (see above), each turtle was tested only on days when it would normally have been fed in accordance with the every-other-day pattern. Thus, the first of the two trials was conducted 2 days after the turtle had last experienced a conditioning session with the rewarded field; the remaining trial was conducted 2 days after the first.

Article

To control for possible daily variations in activity levels, individuals were tested at the same time of day for both trials. At the end of each session, turtles that had been tested that day were fed in the rewarded magnetic field to reinforce the conditioned response.

As with conditioning sessions, turtles began each test period with 20 min in the acclimation field (see above). The magnetic field was then changed to the field being tested for another 20 min. Each test period was recorded using a camera (GoPro) placed directly above the bucket. No observers were present in the room during experiments.

For testing in the mismatched field experiments, each turtle was assigned randomly to one of the two mismatched fields: either the inclination of Maine paired with the intensity of Florida, or the inclination of Florida paired with the intensity of Maine. Each turtle was also tested in the rewarded field (Maine) and in the unrewarded field (Florida).

For experiments involving the magnetic map and radiofrequency fields, turtles were tested once in their rewarded field with radiofrequency and once without, using the conditioning and magnetic field discrimination protocols described here. Half of the turtles were tested first with radiofrequency fields and half were tested first without. For details on radiofrequency field production and measurement, see the section 'Generating radiofrequency fields'.

Data analysis. Videos of the magnetic field discrimination experiments were analysed using BORIS (behavioral observation research interactive software; version 17.13.8)⁶¹. Analyses were carried out blindly by observers unaware of the magnetic field in which each turtle was tested. Before analyses, each observer was trained to recognize turtle dance behaviour, a distinctive food-anticipatory behaviour of captive-reared sea turtles that is characterized by a turtle raising its head near or above the water surface, tilting towards a vertical posture, and often opening its mouth. In addition, turtles often paddle alternately with their front flippers and spin in place, especially in the presence of food (Supplementary Video 1). Analysts recorded the total duration of turtle dancing for each 20-min test period. Each behavioural test was scored by at least two observers working independently. Results from all observers were then averaged.

All statistical computations were completed using R statistical software (version 4.2.2)⁶². Wilcoxon signed-rank tests were used for paired comparisons of turtle responses to the two magnetic fields (rewarded versus unrewarded). For each pair of magnetic fields, the level of turtle dancing in the rewarded field did not differ regardless of which of the two fields was rewarded (Wilcoxon Mann–Whitney, all $P > 0.5$). Thus, turtle responses in the rewarded fields were grouped for each pair of magnetic fields tested; similarly, turtle responses to the unrewarded fields were combined (Figs. 2 and 3a). For each pair of magnetic fields tested, effect size was calculated using Hedge's g , a metric of effect size that accounts for small sample sizes^{63–65}.

As an additional, complementary way of analysing the results of the conditioning treatments, the percentage change in turtle dancing behaviour in the rewarded field was calculated relative to the unrewarded field for each individual turtle (Fig. 3b and Extended Data Fig. 4). Percentage change in turtle dancing behaviour was defined as:

$$\frac{\text{Rewarded field turtle dancing} - \text{unrewarded field turtle dancing}}{\text{Unrewarded field turtle dancing}} \times 100.$$

Given our *a priori* prediction that turtles would dance more in the rewarded field than in the unrewarded field (that is, the percentage change in dancing relative to that in the unrewarded field would be above zero), we used one-tailed Wilcoxon signed-rank tests to investigate changes in responses between the rewarded and unrewarded treatments.

In initial analyses of the mismatched field experiment (Fig. 4b), responses were log transformed and analysed using a linear mixed effects model⁶⁶ so that effects across three treatments could be

assessed. This analysis was predicated on previous findings indicating that turtles detect both inclination and intensity^{19,58,59} and addressed the question of whether turtles might be sufficiently flexible to recognize the rewarded field by using either inclination alone or intensity alone, with an ability to use either interchangeably (much as humans can recognize a familiar individual on the basis of visual appearance, voice or both together). If this is the case, then turtles would be expected to dance just as long regardless of whether they were exposed to the rewarded intensity or to the rewarded inclination; more specifically, turtles should respond equally to the mismatched field with the correct inclination, the mismatched field with the correct intensity and to the rewarded field (with correct inclination and correct intensity). Thus, the two mismatched fields were considered together as one treatment. Log of time exhibiting the turtle dance was the response variable, the magnetic fields (rewarded, unrewarded and mismatched) served as independent variables, and the random variable was turtle identification. Given that field treatment was a significant predictor of time spent turtle dancing (analysis of variance, $F(2,30) = 5.9$, $P = 0.007$), pairwise comparisons, with a Benjamini–Hochberg adjustment to account for multiple groups, were then used to assess differences between pairs of field treatments (Fig. 4b).

In an additional analysis of the mismatched field data (Fig. 4c), we asked whether turtles might have relied: (1) solely on intensity, in which case they should respond only to magnetic fields with the correct intensity; (2) solely on inclination, in which case they should respond only to magnetic fields with the correct inclination; or (3) on both intensity and inclination together, in which case they should respond only to the rewarded field and not to either mismatched field. We calculated the percentage change in time that each turtle spent dancing in the rewarded magnetic field or in a mismatched magnetic field relative to the response of the same turtle in the unrewarded field. Percentage change in turtle dancing behaviour was defined as:

$$\frac{\text{Test field turtle dancing} - \text{unrewarded field turtle dancing}}{\text{Unrewarded field turtle dancing}} \times 100.$$

We predicted that the percentage change in response between a treatment field and the unrewarded field should exceed zero if turtles recognized the treatment as their rewarded field. We therefore used one-tailed Wilcoxon signed-rank tests to determine whether the levels of turtle dancing behaviour in the rewarded field and in each mismatched field were significantly greater than in the unrewarded field (Fig. 4c). We directly compared the results of the rewarded and mismatched fields by using Wilcoxon TOST equivalence tests^{67,68} to assess whether the percentage change in response to the rewarded field was statistically equivalent to the percentage change in the responses to each mismatched field. For equivalence tests, we used the rewarded field as the standard and set the equivalence bound to the raw mean percentage change in turtle dancing behaviour in the rewarded field compared with that in the unrewarded field.

The plots of all data were generated using ggplot2 (ref. 69) and maps were generated using Natural Earth data (free vector and raster map data at <https://naturalearthdata.com>)^{70–72}.

Compass and map assay

Study site and animal collection. This study was conducted in Melbourne Beach, Florida, USA, in 2022. In May and June, loggerhead turtle nests were marked along a 3-km stretch of beach. Using the date of nest deposition, we monitored incubation periods and predicted when turtles were likely to emerge from each nest.

Hatchlings typically emerge from nests at night. On the date when hatchlings were expected to emerge from a nest, we dug gently into the nest by hand several hours before sunset and collected approximately 20 hatchling turtles. The hatchlings were placed inside a Styrofoam cooler to minimize light exposure and then were walked back to the

laboratory space, which was located less than 1.5 km from all nests. Each hatchling was subjected to a brief physical examination. Turtles with physical abnormalities (for example, extra vertebral or lateral scutes, and carapace deformities) or signs of developmental heat stress (for example, lethargy and ocular haemorrhage) were not used in experiments. Animals were maintained in the coolers in the local magnetic field in darkness until experiments began after sunset. For each treatment, we used turtles drawn from 16 different nests, with no more than 4 turtles from a single nest used in the same treatment.

Experimental apparatus. Details of methodology have been previously described^{14,19,58,73}. In brief, experiments were conducted in an outdoor magnetic coil system, consisting of two different 4-coil systems⁷⁴ arranged orthogonally. One coil system controlled the horizontal component of the magnetic field and measured 2.40 m on a side, whereas the second coil system controlled the vertical component of the magnetic field and measured 2.54 m on a side. For each trial, a turtle was placed into a soft cloth harness and tethered to an electronic tracking unit in the centre of a circular experimental arena placed in the centre of the coil system. The fibreglass arena, which measured approximately 1.1 m in diameter at the level where the turtles swam, was filled with fresh water to a depth of about 28 cm. Turtles were tethered to a rotatable tracker arm, which restricted swimming to the centre of the coil (a circle of radius of 33 cm). A white LED light (approximately 420–750 nm; Mouser electronics, <https://www.mouser.com/datasheet/2/239/ltw-42nc5-1175386.pdf>) was fastened to the wall of the arena directly to the east near the water surface. As in previous magnetic orientation experiments with hatchling turtles^{19,40,58,59,75}, the light was kept on for a short period at the start of each trial, but was then turned off so that turtles swam in total darkness during the period when magnetic orientation was monitored (see below). To ensure that turtles were in darkness when the LED was turned off, the top of the fibreglass arena was covered with a plywood lid (1.8 cm in diameter) that was fastened to the arena with non-magnetic bolts during all experiments. A layer of opaque, compressible foam rubber between the plywood and the rim of the tank sealed any small gaps between the lid and tank. Finally, the entire tank and lid were covered with four layers of opaque black plastic sheeting held in place around the tank with non-magnetic elastic bands. All electronic equipment, for example, computers and power supplies, was kept in a building approximately 20 m from the coil. Power supplies provided current to the coil system and LED light. The electronic tracking unit was controlled by custom software.

The magnetic fields in the arena were determined by averaging five independent measurements using a Meda tri-axial magnetometer (model FVM-400). Measurements of the local Melbourne Beach magnetic field indicated an inclination of 56.5° and an intensity of 44.6 μ T. The magnetic field used to approximate conditions near the Cape Verde Islands had an inclination of 22.9° and an intensity of 34.1 μ T. The experimental field (Cape Verde) was selected on the basis of estimates provided by the World Magnetic Map Model for July 2022 (the month when the experiment began) using latitude 20.0° N and longitude 30.5° W. As in the conditioning experiments (map assay), declination was held constant in all magnetic fields.

Experimental protocol. All trials were run at night (between 20:30 and 02:00) when hatchling turtles are most active. During experiments, water temperature was approximately 26–28 °C. Each turtle was tethered to a rotatable tracker arm affixed to a post in the centre of the arena. As the turtle moved the tracker arm, a digital encoder relayed orientation data to a computer every 10 s. Each turtle began its trial in the local magnetic field of Melbourne Beach, Florida and was allowed to establish a course towards a dim light located in magnetic east. Healthy hatchlings capable of migrating offshore typically maintain a highly consistent heading as they swim towards the light; thus, hatchlings that did not swim towards the light were excluded from experiments and replaced with more robust

individuals. After 10 min, the light was turned off for the remainder of the trial, and the magnetic field was simultaneously changed to a field replicating one near the Cape Verde Islands. At this point, the turtles were in complete darkness and reliant on orienting with their magnetic compass in response to magnetic map information^{14,15,19,58,73}. Turtles were allowed to acclimate to the new field for 3 min. If a turtle became inactive when the light was turned off and failed to move through at least three quadrants of the arena during the acclimation period, the trial was terminated without proceeding to data collection. After the acclimation period, orientation data in the Cape Verde field were collected for 5 min. A mean bearing was calculated for each turtle for this 5-min test period. During the test period, turtles experienced either: (1) the Cape Verde magnetic field, or (2) the Cape Verde magnetic field with radiofrequency fields present. These two treatments were interspersed each night. Sample sizes were chosen to approximate those used in similar, previously published studies with sea turtles^{14,19,59}.

All statistical computations were completed using R statistical software^{62,76}. Circular statistics were used for comparisons of turtle orientation responses in the Cape Verde field with and without radiofrequency fields.

Generating radiofrequency fields

Oscillating magnetic fields in the radiofrequency range were produced by driving currents through circular single-loop transmission antennas. A transmission antenna composed of one single loop of insulated copper wire (12 AWG (American wire gauge)) for the map assay, and 14 AWG for the compass and map assay) encircled the arena in which the turtle was tested. The antenna was positioned so that it was level with the surface of the water and was connected to a function generator (map assay) or a function generator and radio amplifier (compass and map assay). Agilent 33220A and Rigol DG822 function generators were used for the two respective experiments. Broadband electronic noise from the function generators produced oscillating vertical magnetic fields in the total range of 0–15 MHz, but primarily between 0.1 and 10 MHz, the range of frequencies used in most previous studies⁶.

Before constructing the antenna systems, the predicted magnetic field strengths and profiles were computed numerically using COMSOL Multiphysics⁷⁷ and also calculated analytically using Mathematica (Wolfram Research, Mathematica, version 13.3 (2023)). Both methods yielded consistent results and indicated that, in the plane of the transmission antenna, the oscillating magnetic field was expected to be weakest in the centre and to increase non-linearly with the radius to the side of the arena. At a distance half a radius from the centre, calculations indicated that the magnetic field increased by 24.6%. Vertical displacements from the plane on the scale of a tenth of the radius decreased the magnetic field strength less than 5%.

Procedures for measuring the fields and corroborating the predicted values, as well as additional details specific to each set of experiments, are described below.

Oscillating magnetic field measurements. Measurements of the magnetic field spectrum were taken using a 12-cm-diameter circular receiving antenna consisting of one loop of 12 AWG insulated copper wire. The receiving antenna was connected by a 1-m-long BNC 50 Ω cable to an oscilloscope with 1 M Ω input impedance. The receiving antenna was oriented so the normal vector to the antennal plane was aligned with the vertical magnetic field. A 50 Ω 3 dB attenuator was placed in series with the antenna to remove resonance and flatten the antenna frequency response in the frequency range of interest. Oscillations of the total magnetic flux through the loop induced a voltage on the receiving antenna. The induced voltage on the receiving antenna was digitized as a time series by the oscilloscope and saved to file. The time-series data were converted to a voltage spectral density by taking the Fourier transform using NumPy (version 1.24.0)⁷⁸. This was then converted to the magnetic flux spectral density using Faraday's law of

Article

induction and by performing a lumped-element circuit analysis on the receiving antenna–oscilloscope circuit. Integration of the magnetic flux spectral density gives the root-mean-square magnetic flux density over the frequency range of interest⁶.

Measurements with voltages driven at single frequencies and with variable amplitudes were used to calibrate the receiving antenna setup and validate our magnetic field calculations. Predicted and measured magnetic flux densities agreed to the 1.9–7.3% level for coherent sinusoidal test signals in the targeted frequency range of 0.1–10 MHz. Additional measurements with the loop antenna located at various positions in and above the experimental tank confirmed the calculated results for the radial and axial dependence of the magnetic field.

Oscillating magnetic fields produced for the map assay experiments. In the map assay experiment, the transmission loop antenna used to generate the broadband noise signal consisted of one loop of 12 AWG insulated copper wire. The loop was 33 cm in diameter and was wrapped around a 20-l plastic bucket, which served as the experimental arena. The function generator (Agilent 33220A) was located approximately 2 m from the magnetic coil system and was kept on during all trials to ensure that turtles were always exposed to the same fan noise regardless of treatment. The function generator output was set to the noise setting with a peak-to-peak amplitude of 10 V. During control trials, the output was turned off so that no oscillating magnetic field was produced at any point during the trial. During experimental trials, the output was turned off during the 20-min acclimation period but was turned on during the 20-min test period.

Measurements of the oscillating magnetic fields were made using a Tektronix TDS 2024B oscilloscope with the insulated receiving antenna immersed in the water where turtles were tested. The root-mean-square magnetic flux measured in the centre of the map assay arena was 172 nT in the targeted 0.1–10 MHz range (Extended Data Fig. 5a), with a standard deviation of 7 nT from 10 repeated measurements. From the waterline to the bottom of the arena, the magnetic field decreased less than 25%. Thus, a turtle experienced similar fields whether at the surface or submerged. A turtle that moved from side to side in the arena also experienced relatively little change; the range of magnetic flux across the arena was 125–250 nT. When the transmission loop antenna was turned off, the background root-mean-square magnetic flux was measured to be less than or equal to 9.6 nT in the 0.1–10 MHz frequency range.

Oscillating magnetic fields produced for the compass and map assay experiments. In the compass and map assay experiments, the loop antenna used to generate the broadband noise signal consisted of one loop of 14 AWG insulated wire. The loop was 114 cm in diameter and was secured directly to the outside of the experimental arena at the level where hatchling turtles swam in these trials. The function generator (Rigol DG822-25) used to produce the broadband noise signal was kept inside a nearby building along with the computer and power supplies used to control the magnetic coil system. A high-power amplifier (LZY-22X+, Mini-Circuits), with an operational bandwidth up to 200 MHz, was used to increase the power from the function generator. The function generator output was set to the noise setting with a peak-to-peak amplitude of 4 V. This setting was selected so that the measured strength of the oscillating magnetic fields produced in the compass and map assay experiments approximately matched those produced in the map assay experiments. During control trials, the function generator and amplifier were kept off to avoid overheating the amplifier. During experimental trials (with broadband noise), the function generator and amplifier output were turned on during the 5-min test period, but not during the light acclimation period or the 3-min acclimation period in the Cape Verde magnetic field.

Oscillating magnetic fields were measured using a Rigol DS1102Z-E oscilloscope with the receiving antenna immersed in the water where

turtles were tested. The root-mean-square magnetic flux measured in the area where turtles swam was 141 nT in the targeted 0.1–10 MHz range, with a standard deviation of 6 nT from 8 repeated measurements (Extended Data Fig. 5b). The spectral feature present at 2 MHz (Extended Data Fig. 5b) appears to be resonances between the antennas and the surrounding magnetic coil system, as the feature was absent in laboratory tests conducted without the surrounding magnetic coil. In contrast to the map assay experiments, turtles were tethered at the surface of the water; thus, the magnetic fields at the bottom of the tank were not relevant. The range of magnetic flux experienced as the turtles swam around the tank was in the range of 100–200 nT. The background magnetic flux was measured to be less than or equal to 7.8 nT in the 0.1–10 MHz frequency range.

Electric field calculations. Although responses to oscillating magnetic fields are considered to be a diagnostic test for the radical pair mechanism of chemical magnetoreception⁴, all time-varying magnetic fields induce electric fields. In the near field limit where we operated, this induced electric field is relatively small. In addition, electric fields are not the element of radiofrequency fields theorized to affect the radical pair mechanism⁴. For the sake of completeness, however, we provide a calculation of the induced electric fields in our setup. Assuming that the magnetic field is approximately radially symmetric, the electric field would also be radially symmetric with only a radial component. The electric field strength was therefore calculated as a function of radius using the Maxwell–Faraday equation in integral form. In the region where turtles swam, the root-mean-square electric field was calculated to be $9.5 \pm 0.4 \text{ mV m}^{-1}$ for the map assay experiments and $27.2 \pm 1.1 \text{ mV m}^{-1}$ for the compass and map assay.

Ethics statement. Research was approved by the UNC Institutional Animal Care and Use Committee (protocols 17-929.0, 20-248.0 and 21-091.0), the Florida Fish and Wildlife Conservation Commission (permit MTP-22-065) and the North Carolina Wildlife Resources Commission (permit ST44).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

There are no restrictions on data availability. Access to the data can be found on GitHub (https://github.com/kaylago/GoForthetal_Learned-MagneticMapCuesandTwoMechanismsofMagnetoreceptioninTurtles.git). Source data are provided with this paper.

Code availability

Custom-written software by A.H. facilitated data collection in the compass and map assay experiments, but the software was not central to the research or conclusions. The code can be accessed on GitHub (https://github.com/radiotech/Caretta2_Encoder).

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Author contributions The research plan was conceived by K.M.G., K.J.L. and C.M.F.L. K.M.G. conducted the conditioning experiments and data analyses with input from K.J.L. and C.M.F.L. K.M.G., D.S.L., T.L.H., K.J.L. and C.M.F.L. conducted the compass and map assay experiments. A.H. wrote the software used in some experiments. A.G. and R.H. generated and measured the radiofrequency fields. K.M.G., K.J.L. and C.M.F.L. drafted the manuscript, which was revised with input from all authors. This research was supported by the Air Force Office of Scientific Research grant FA9550-20-1-0399 to K.J.L. and the National Science Foundation grant IOS-1456923 to K.J.L. and C.M.F.L. A.G. was supported by the National Science Foundation grant OISE-1743790. R.H. and A.G. were supported by the US Department of Energy, Office of Science, Office of Nuclear Physics grants DEFG02-97ER41041 and DEFG02-97ER41033.

Competing interests The authors declare no competing interests.

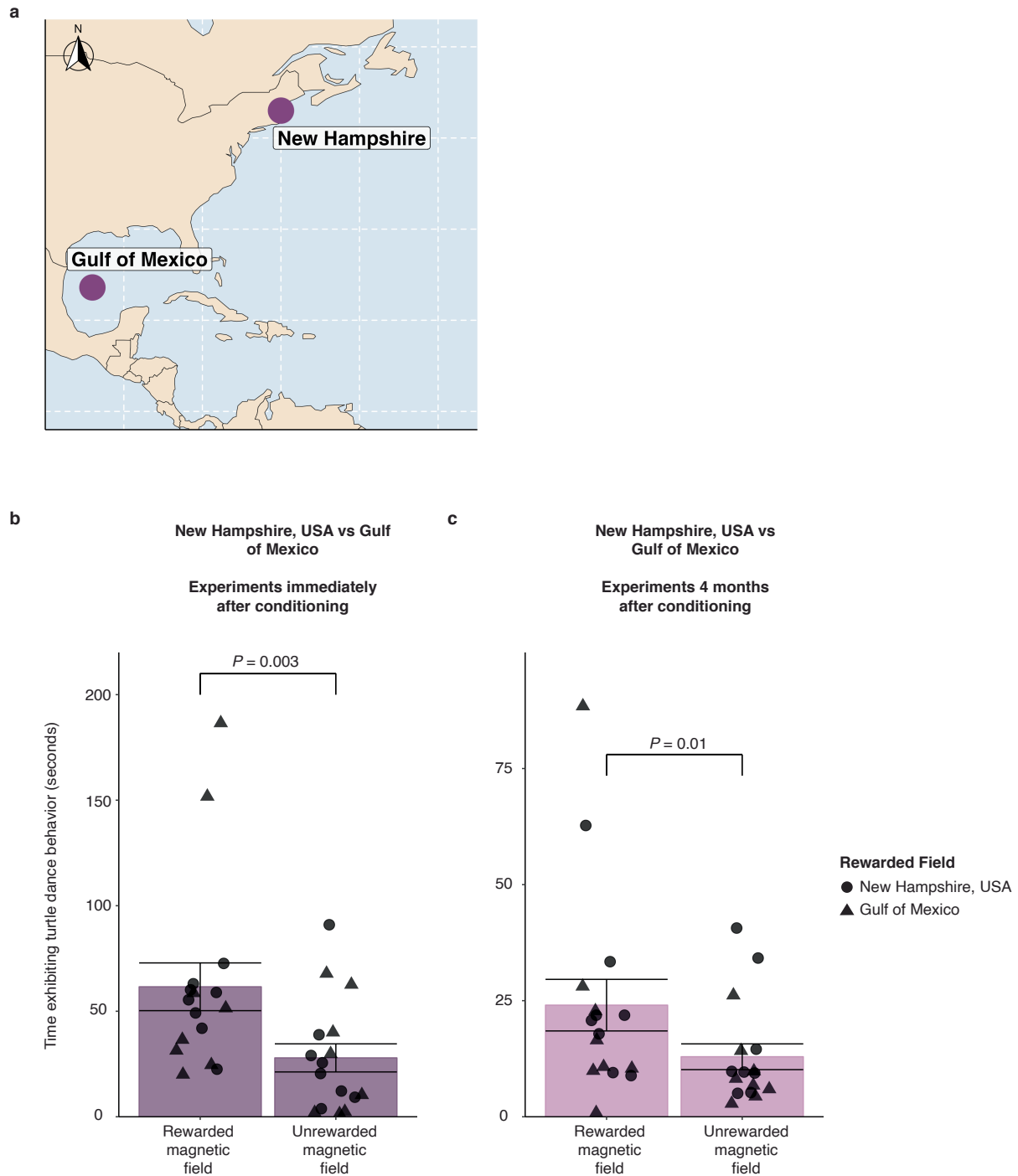
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-024-08554-y>.

Correspondence and requests for materials should be addressed to Kayla M. Goforth.

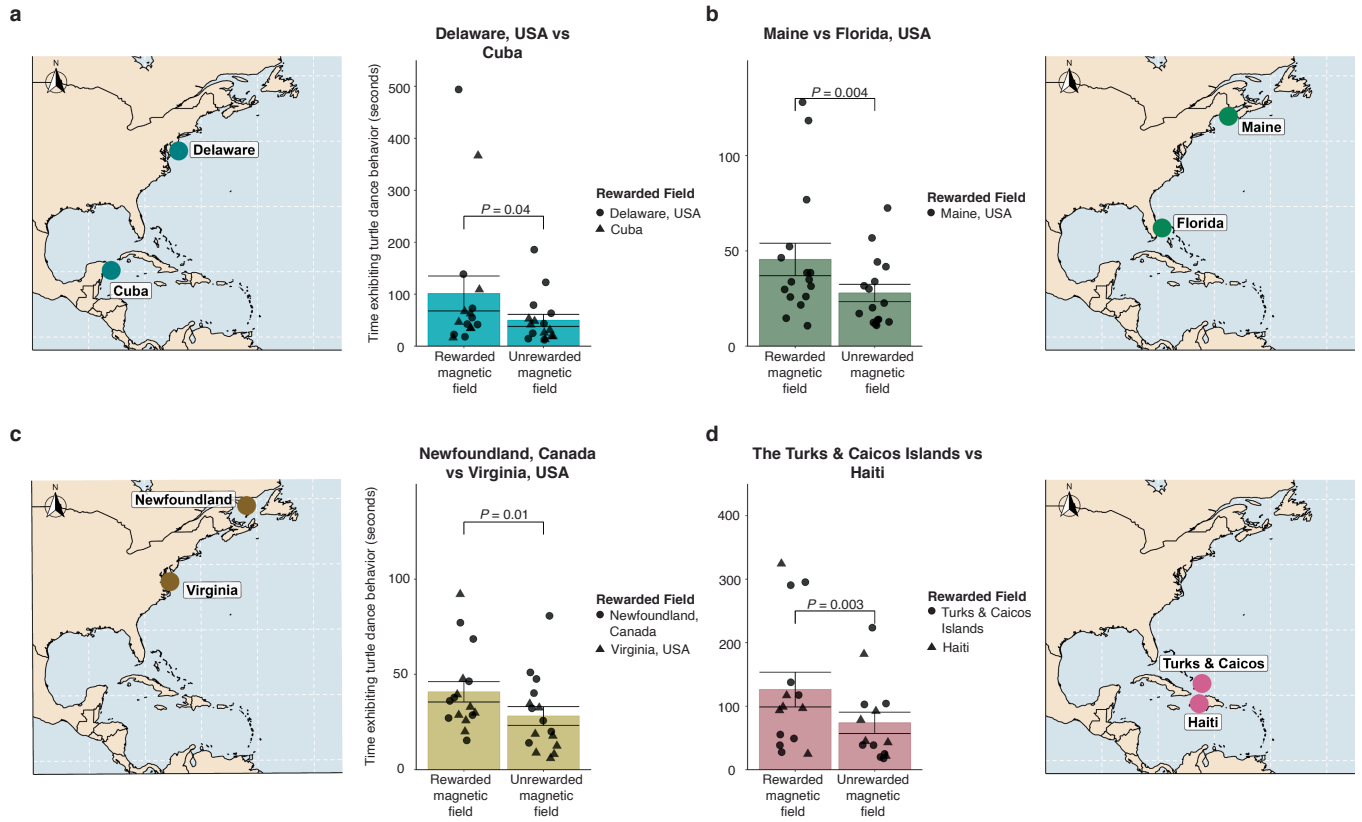
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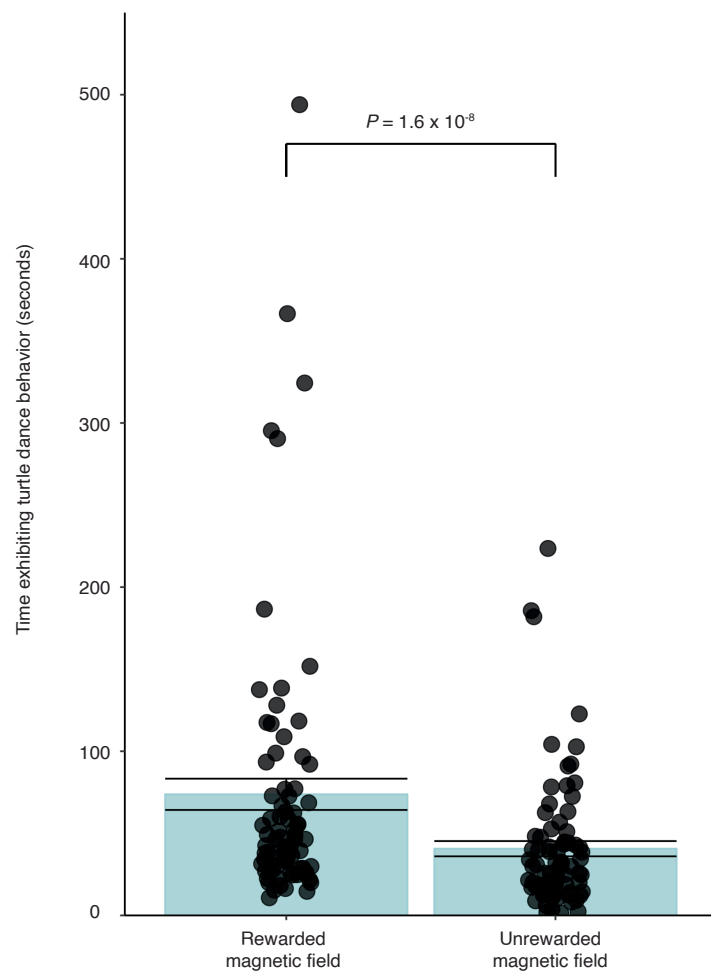
Extended Data Fig. 1 | Results from Fig. 1 plotted on a linear scale. Turtles learned to discriminate between magnetic fields replicating ones that exist near New Hampshire, U.S.A. and in the Gulf of Mexico. (a) Map showing relative locations of the two treatment fields. The map was created using Natural Earth (<https://www.naturalearthdata.com>; credit Tom Patterson and Nathaniel Vaughn Kelso). (b) In tests conducted immediately after the conditioning period, turtles exhibited significantly higher levels of turtle dance behavior when experiencing the field in which they had been fed (two-tailed Wilcoxon

signed-rank test, $w = 123$, $p = 0.003$, Hedge's $g = 0.88$, $n = 16$, ● = turtles rewarded in the New Hampshire field, ▲ = turtles rewarded in the Gulf of Mexico field). See Methods for details of analysis. (c) Turtles were tested a second time, four months after the initial experiments, without experiencing either the rewarded or unrewarded field in the interim. Turtles still discriminated between the two fields (two-tailed Wilcoxon signed-rank test, $w = 118$, $p = 0.01$, Hedge's $g = 0.62$, $n = 16$). Error bars represent standard error.

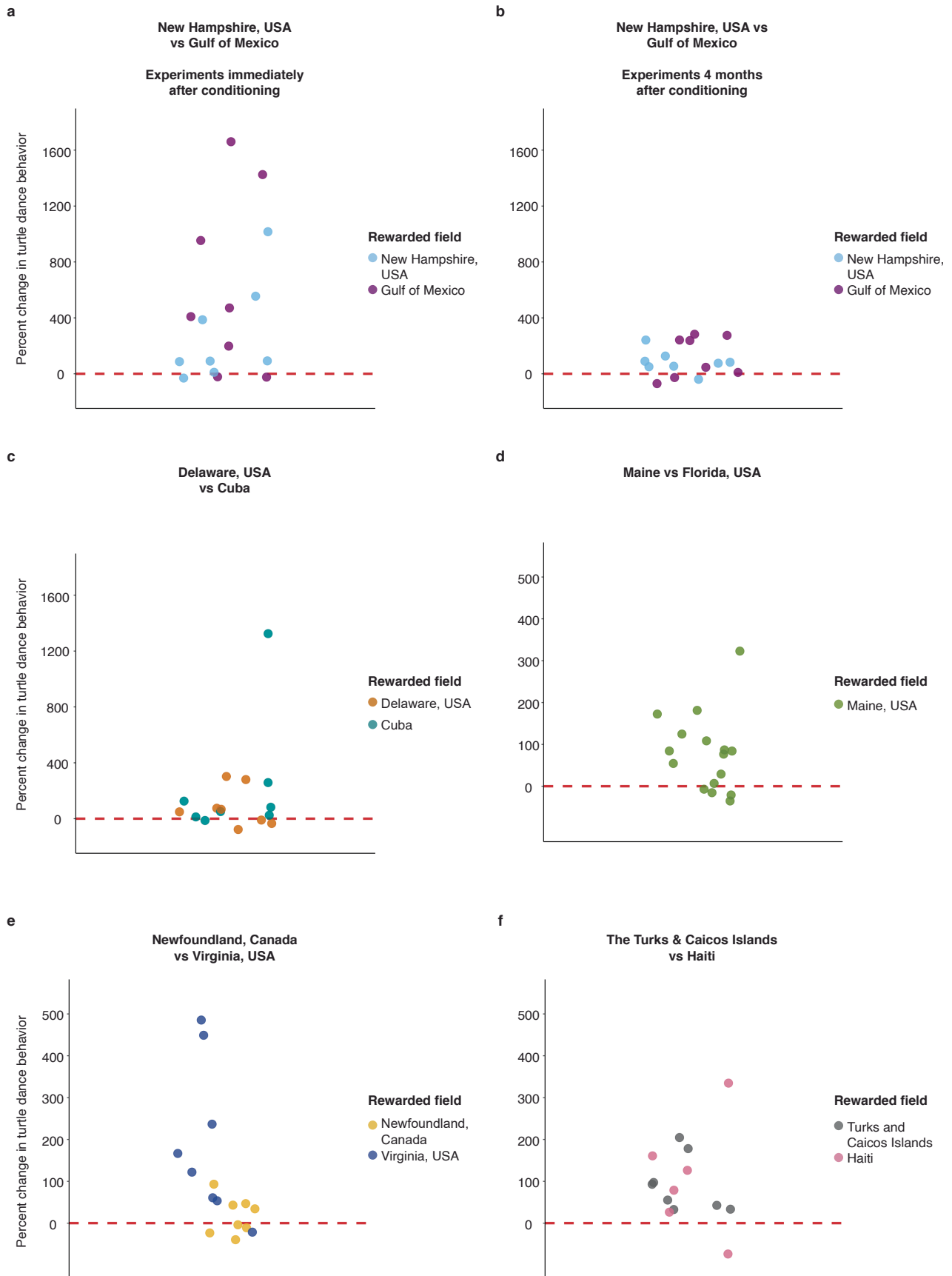


Extended Data Fig. 2 | Results of additional map assay experiments plotted on a linear scale. In four additional experiments, turtles discriminated between a magnetic field in which they were fed and one in which they were not. Turtles differentiated between magnetic fields that exist near: (a) Delaware, U.S.A. and Cuba (two-tailed Wilcoxon signed-rank test, $w = 108$, $p = 0.04$, Hedge's $g = 0.50$, $n = 16$); (b) Maine and Florida, U.S.A. (two-tailed Wilcoxon signed-rank test, $w = 121$, $p = 0.004$, Hedge's $g = 0.63$, $n = 16$); (c) Newfoundland, Canada and Virginia, U.S.A. (two-tailed Wilcoxon signed-rank test, $w = 115$, $p = 0.01$, Hedge's $g = 0.60$, $n = 16$); and (d) the Turks and Caicos Islands and Haiti

(two-tailed Wilcoxon signed-rank test, $w = 97$, $p = 0.003$, Hedge's $g = 0.60$, $n = 14$). The data in (c) represent a second conditioning experiment conducted with the same turtles used in (b) and thus indicate that turtles can learn magnetic fields that exist at multiple locations. For each pair of magnetic fields, the rewarded field for the turtle is indicated by either ● or ▲ as indicated on the figure. Remaining conventions as in Fig. 1. The maps were created using Natural Earth (<https://www.naturalearthdata.com>; credit Tom Patterson and Nathaniel Vaughn Kelso).



Extended Data Fig. 3 | Data from all map assay experiments (Fig. 3a) plotted on a linear scale. Turtles learned to discriminate between a magnetic field in which they received food and one in which they did not (two-tailed Wilcoxon signed-rank test, $w = 2676$, $p = 1.6 \times 10^{-8}$, Hedge's $g = 0.50$, $n = 78$). Conventions as in Fig. 3a.

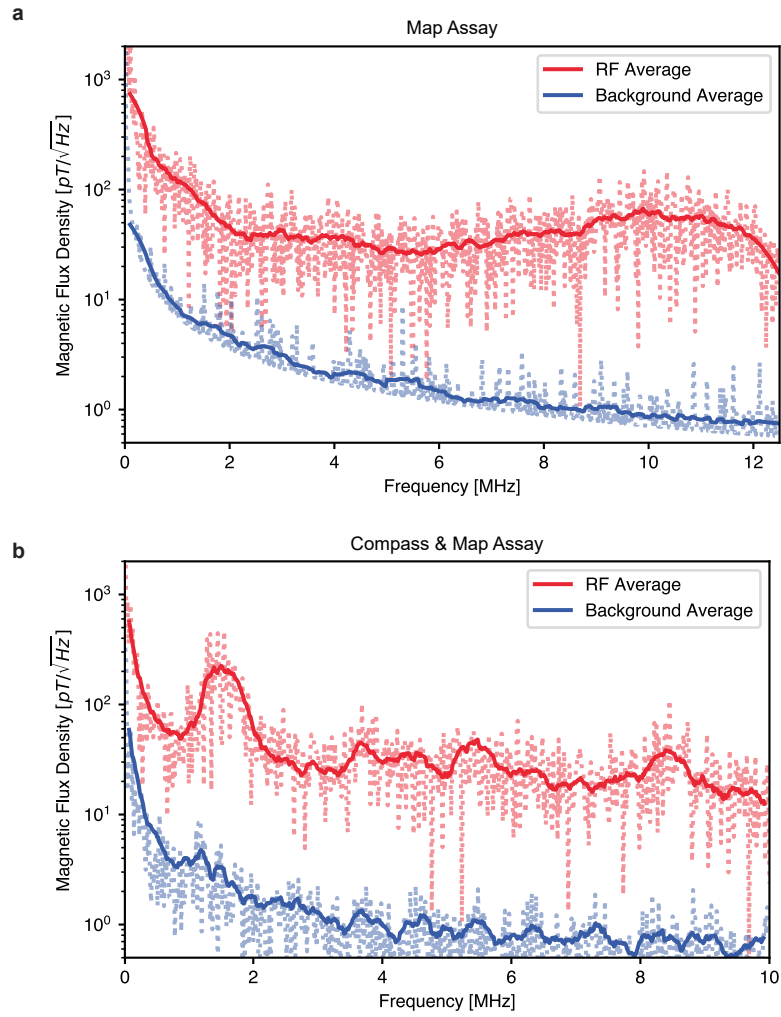


Extended Data Fig. 4 | See next page for caption.

Extended Data Fig. 4 | Percent change in turtle dancing responses for all turtles. Percent change = $\frac{\text{Rewarded field turtle dancing} - \text{Unrewarded field turtle dancing}}{\text{Unrewarded field turtle dancing}} * 100$.

Red dotted lines indicate 0% change relative to the unrewarded field. Dots represent the percent change for individuals; dot color corresponds to the rewarded magnetic field as indicated on the figure. All data were analyzed with one-tailed Wilcoxon signed-rank tests. (a) Turtles conditioned to magnetic fields near New Hampshire, U.S.A. and the Gulf of Mexico had a percent change in dancing behavior significantly greater than zero ($w = 127, p = 0.0005$, Hedge's $g = 0.80, n = 16$). (b) When these same turtles were tested four months after conditioning ended, without exposure to either field in the interim, percent change in dancing was again significantly greater than zero ($w = 124,$

$p = 0.001$, Hedge's $g = 0.85, n = 16$). (c) Turtles conditioned to Delaware, U.S.A. and Cuba had a percent change in dancing behavior significantly greater than zero ($w = 118, p = 0.004$, Hedge's $g = 0.45, n = 16$). (d) Turtles with a rewarded field of Maine, U.S.A. had a percent change in dancing significantly greater than zero ($w = 121, p = 0.002$, Hedge's $g = 0.80, n = 16$). (e) Turtles conditioned to Newfoundland, Canada and Virginia, U.S.A., had a percent change in dancing significantly greater than zero ($w = 120, p = 0.003$, Hedge's $g = 0.63, n = 16$). (f) Turtles conditioned to Haiti and the Turks and Caicos had a percent change in dancing significantly greater than zero ($w = 99, p = 0.0009$, Hedge's $g = 0.94, n = 14$). Collectively, these analyses of percent change corroborate the findings based on raw data in Figs. 1 and 2.



Extended Data Fig. 5 | Measured RF magnetic flux at water level in the testing environments in the two RF experiments. (a) Magnetic flux density of the broadband oscillating magnetic fields, as well as the background magnetic field fluctuations, produced during the map assay experiments. Single runs (a single measurement of the field) are displayed as vertical dashed lines and are digitized with 25 MHz sampling frequency and a 2048 sample buffer. Measurements extended to 12 MHz but only values in the targeted range

(0.1–10 MHz) were included in calculations. **(b)** Magnetic flux density of the broadband magnetic fields produced and the background magnetic field fluctuations during the compass & map assay experiments. Single runs are displayed as vertical dashed lines and are digitized with 20 MHz sampling frequency and a 1200 sample buffer. In (a) and (b) solid lines represent the average magnetic noise density, calculated from 10 and 8 repeated measurements respectively.

Extended Data Table 1 | Results of the linear mixed effects model for the mismatched field experiments

Fixed Effects	Coefficient	Standard Error	Benjamini-Hochberg pairwise comparisons to rewarded field
Intercept	3.75	0.2	NA
Unrewarded field	-0.63	0.2	0.01
Mismatched field	-0.60	0.2	0.01

See Methods for details. Benjamini-Hochberg pairwise comparisons are with respect to the rewarded field.

Extended Data Table 2 | Magnetic fields used to approximate conditions in different geographic areas

Field	Inclination (degrees)	Intensity (microtesla)	Latitude/Longitude for field estimate	Year(s) field was used
Gulf of Mexico	53.4	43.1	24 N, -94 W	2017 autumn
New Hampshire, U.S.A.	67.3	52.7	43.3 N, -70 W	2017 autumn
Delaware, U.S.A.	64.5	51.1	38.7 N, -75 W	2018 autumn
Cuba	49.0	41.1	20.2 N, -86 W	2018 autumn
Maine, U.S.A.	66.6	51.4	43.0 N, -67.5 W	2019 autumn
Florida, U.S.A.	54.3	43.8	26.0 N, -79.3 W	2019 autumn
Virginia, U.S.A.	63.7	50.2	37.4 N, -75.5 W	2020 spring (same cohort as 2019 autumn)
Newfoundland, Canada	69.6	53.4	49 N, -61.8 W	2020 spring (same cohort as 2019 autumn)
Turks and Caicos	48.7	39.6	21.8 N, -72.2 W	2020 autumn
Haiti	45.3	37.5	18.8 N, -71.5 W	2020 autumn
Acclimation	60.4	47.6	not applicable	All years
Maine inclination, Florida intensity	66.5	43.6	not applicable	2019 autumn
Florida inclination, Maine intensity	54.2	51.3	not applicable	2019 autumn

For each magnetic field, values are based on 4–8 measurements made with a Meda tri-axial magnetometer (model FVM-400) in the area where turtles were positioned during experiments. The experimental fields were selected using estimates from the International Geomagnetic Reference Field (IGRF) model. The acclimation field was the magnetic field to which all turtles were exposed at the start of each trial when turtles were first moved into the coil (see Magnetic field conditioning protocol in Methods). This acclimation field mimicked that of the husbandry facility and differed slightly from the natural ambient magnetic field. Declination (the difference between magnetic north and geomagnetic north) was held constant in all magnetic fields.

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Software and code

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Data collection	Custom written software by coauthor Andrew Harvey facilitated data collection in the compass & map assay experiments but the software was not central to the research or conclusions. Code can be accessed at https://github.com/radiotech/Caretta2_Encoder
Data analysis	BORIS (Behavioral Observation Research Interactive Software) Version 17.13.8 was used to analyze data from the map assay experiments. R Statistical Software Version 4.2.2 was used to analyze data from both the map assay experiments and the compass & map assay experiments. COMSOL Multiphysics, Mathematica version 13.3, and NumPy version 2.1.3 were used in the measurement of RF fields.

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For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size For the map assay experiments, sample size was based on the maximum number of turtles (14-16) that could be housed in our facility at UNC at any one time, as well as on sample sizes used in previous studies of reptile conditioning. Analyses confirmed that a sample size of 14-16 individuals was sufficient to demonstrate differences between groups (e.g., Figs. 1,2). For the compass and map assay experiments, sample sizes were determined based on previous published experiments using the same compass and map assay, which had approximately 25 turtles per group - for example, see Lohmann et al., 2001; Putman et al., 2011; and Lohmann and Lohmann, 1996.

Data exclusions No data were excluded.

Replication Conditioning experiments (map assay) were replicated 5 times, with 5 different cohorts of turtles. The compass & map assay protocol is well established and has been used in many (>10) previous experiments. In particular, the Cape Verde magnetic field has previously been shown to elicit oriented swimming, and the control group (Cape Verde magnetic field without RF) represents a replication of the findings from Putman et al., 2011. Orientation responses to the Cape Verde field with RF were collected in just this present study. All attempts at replication were successful.

Randomization Turtles in each cohort were randomly assigned to one of two groups for the map assay experiments. During behavioral experiments, half the turtles were tested in the rewarded field first, and half were tested in the unrewarded field first. For the compass & map assay experiments, we alternately tested turtles in the control treatment without radiofrequency, and in the experimental treatment with radiofrequency throughout each night of testing.

Blinding For the map assay experiments, observers analyzing the data were blind to the magnetic field treatment. Results from all observers were then averaged. For the compass & map assay experiments, data were collected by computer and automatically analyzed to avoid any possible bias.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input type="checkbox"/>	<input checked="" type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern
<input checked="" type="checkbox"/>	<input type="checkbox"/> Plants

Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

Animals and other research organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research, and [Sex and Gender in Research](#)

Laboratory animals	No laboratory animals were used in this study.
Wild animals	For the map assay experiments, loggerhead turtles (<i>Caretta caretta</i>) were collected from Bald Head Island, North Carolina, USA as hatchlings. Turtles were collected at 0 days of age, placed in closed, padded containers, and transported back to the laboratory via car. Turtles were between 3 months to 1 year at the time of experiments. Following all experiments turtles were released unharmed into the ocean. For compass and map experiments, loggerhead turtles (<i>Caretta caretta</i>) were collected from Melbourne Beach, Florida, USA prior to emerging from their nest (0 days of age). Turtles were placed into closed, padded containers and walked back to the laboratory site. After being tested in behavioral experiments all turtles were released unharmed into the ocean.
Reporting on sex	In juvenile and hatchling sea turtles sex cannot be determined via any external morphology. Thus we could not record sex data from turtles used in these studies.
Field-collected samples	The study did not involve samples collected from the field.
Ethics oversight	Research was approved by the UNC Institutional Animal Care and Use Committee (IACUC; Protocols 17-929.0, 20-248.0, and 21-091.0), the Florida Fish and Wildlife Conservation Commission (permit MTP-22-065), and the North Carolina Wildlife Resources Commission (permit ST44).

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A